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THE FOSSIL FLORA OF IOWA COAL BALLS

IV. LEPIDOCARPON

BY
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Seeds and seed-like bodies have been observed in all of the coal ball floras of the world. Krick (7), Reed (10), Schopf (11), and Darrah (2) have recorded numerous forms from various American localities. Recently in the progress of our investigation of Iowa coal balls, large numbers of smooth seeds or seed-like structures without any prominent scars or markings were isolated from the matrix by mechanical means. These rather large organs are somewhat flattened and elongate. A typical specimen is approximately 12 mm. long, 8.5 mm. wide, and 7 mm. thick in a median plane. Many, however, are considerably larger. Serial sections were prepared from four specimens for routine examination, and it appears that these seed-like structures are really sporangia similar to those characteristic of the extinct arborescent lycopods, particularly the so-called *Lepidocarpon* alliance.

The best preserved of the seed-bearing Lepidodendrids constitute the genus *Lepidocarpon*, which has been known for nearly a century, although for a long time its true relationship was not understood. In all of the species attributed to this group, the megaspore, which produces its gametophyte endosporally, is retained within integumentary tissues formed from the sporophyll. Even when

the specimens are isolated from the strobili which bear them, they always have this combination of structures. Thus there is a point of distinction between these seed-like organs and a typical seed, that is to say, in *Lepidocarpon* the sporophyll forms an integument and is shed as part of the "seed."

A considerable number of species attributed to *Lepidocarpon* have been described (7, 11, 13), all of which have been collected in rocks of Carboniferous age. They have proved to be of considerable abundance both in Europe and America. A closely related genus was described by Schopf (11) under the name *Illiniocarpon*, but the degree of difference between this form and that of *Lepidocarpon* is not great. The two best known species of *Lepidocarpon* are *L. lomaxi* Scott and *L. wildianum* Scott. The strobili of both of these resemble closely the usual *Lepidostrobus* type, but each megasporangium contains only one mature megaspore. Some of the species also contain three abortive spores. The sporophyll or "bract" forms an integument around the megasporangium, but a micropylar slit remains unclosed. The sporangium has a heavy wall and contains a tough megaspore membrane. The seeds became detached after attaining great size and an advanced degree of tissue differentiation. It is interesting to observe that the seeds of *Lepidocarpon lomaxi* were considered by paleobotanists for many years to be those of a gymnosperm (*Cordaicarpon anomalum* Williamson). Among living pteridophytes no equivalent structures have been observed, although in *Selaginella* the gametophyte develops within the megaspore, forming a living multicellular body, but it usually thrusts through the triradiate crest in the spore wall. No intimate relationship between the spore and the sporangium exists. On the other hand, among many extinct lycopods the sporangium produces one functional megaspore which

develops within the sporangium and fills the sporangium nearly completely, although a central cavity sometimes remains.

In 1914, Kidston (6) described a small strobilus of *Lepidocarpon westfalicum* from the upper Carboniferous of Staffordshire. This is a particularly instructive specimen because the strobilus is said to contain a large number of "ripened" seeds borne spirally upon an axis. The seeds are quite small attaining a length of only 2 to 3 mm. and a thickness of slightly less. We have found in Iowa a single strobilus of *Lepidocarpon lomaxi* in which the seeds are much larger, as a matter of fact attaining a length of nearly 4.5 mm. A comparison of isolated specimens of *L. lomaxi* with those attached in the strobilus has shown clearly that those not yet shed from the cone are immature rather than ripened. The average length of those which have been shed is nearly 6 mm. The histological detail preserved in the megaspores which are still enclosed in their sporangia and sporophyll never demonstrates the advanced degree of differentiation encountered in the isolated specimens. The diameter of the strobilus of *Lepidocarpon westfalicum* Kidston is approximately 1.5 cm. On the individual seeds there is a smooth pit at the basal end which marks the place where the sporangium was attached distally upon the sporophyll.

In 1936, Miss Reed (10) reported on the nature of isolated specimens of *Lepidocarpon*. A single vascular strand traverses the full length of the sporophyll. The sporangial wall is described as having two layers, each averaging three cells in thickness. Both layers, however, are composed of thick-walled isodiametric cells and at first appearance look much alike, the epidermis being only slightly differentiated from the hypodermis. According to her description the sporangium does not have a hypodermis with the distinct palisade appearance of

Lepidocarpon lomaxi Scott. There is an inner layer of thin-walled elongated cells. The megaspore grows to great size and is the single functional member of a tetrad of four spores. In one of her specimens Miss Reed recognized three aborting megaspores, and shows conclusively that they did not disintegrate immediately following inception, but that there was a relatively short growth period for all four megaspores, the proximal spore soon gaining ascendency over the others. In time, the larger of the spores seems to fill the whole cavity. Often, the megaspore membrane is collapsed. Miss Reed notes that never in her experience has she found gametophytic tissue; fragments of tissue which occur occasionally inside the membrane are intruded. She has developed this idea further and argues that the conventional opinion that *Selaginella* foreshadows seed structure is erroneous. She concludes that *Lepidocarpon* is a sporangium containing a living dependent gametophyte.

Several years ago Schopf (11) described impressions of *Lepidocarpon mazonense* from Mazon Creek in northern Illinois. It appears that this interesting species is very abundant, for he was able to collect forty specimens in a few visits to the locality. Prior to this discovery little was known of the variability or the gross form of the sporangium and its associated sporophyll in *Lepidocarpon*. In a more recent contribution Schopf (in Janssen (5), pp. 39–45) added still more information on these structures. He described *Lepidocarpon corticosum* (Lesquereux) Schopf as "a seed structure 11 mm. long and 7.5 mm. tall" borne upon a sporophyll of medium size, with the integumentary structures of the seed attached along a ventral extension of the pedicel enclosing the seed. The proximal end of the pedicel merges with a "splinter" of the former cone axis. The functional or seed-megaspore is 7 mm. long and 3.75 mm. broad; the broader end of

the asymmetrical spore is toward the anterior end of the seed. The megaspore membrane has a characteristic fibrous texture.

Schopf compared *Lepidocarpon corticosum* with *Cantheliophorus* Bassler (Bot. Gaz. Vol. 68, pp. 73–108, 1919) and concluded that most, if not all, of the fertile sporophylls attributed to *Cantheliophorus* should be transferred to *Lepidocarpon*. However, inasmuch as a number of sporophylls of the *Cantheliophorus* type as well as sporangia of the *Lepidocystis* type (White 14) bear many megaspores of the familiar "Triletes" type, it is not possible to accept these transfers until a critical revision of all of the species has been made.

The seed megaspore of *Lepidocarpon* has been named *Cystosporites* by Schopf (12) and he finds it to be a very persistent and abundant form among the microfossils of certain coals of Illinois. The spore is always rather ovoid, elongate and sac-like, varying in its greatest length up to nearly 10 mm. The spore membrane has a characteristic fibrous construction which is densely matted and is thicker and more dense at the distal end. Frequently there are abortive spores which for a time remain attached to the apex of the fertile member and are appressed to the triradiate crest of the functional spore. These abortive spores become detached as the seed megaspore enlarges. They vary greatly in size and when still small are nearly spherical in shape.

One may question the propriety of bestowing a generic name upon isolated spores which are referable to some plant already possessing a generic name. There is no convincing reply to this question. From a botanical and nomenclatorial point of view there would seem to be no justification for a new generic name, but on the other hand, in investigations on the microfossil content of coals, one is dealing exclusively with isolated objects for which

EXPLANATION OF THE ILLUSTRATIONS

PLATE I. LEPIDOCARPON GLABRUM *Darrah sp. nov.* A single seed, embedded in a coal ball, showing the lustrous smooth wall of the sporangium. Shuler Mine, Waukee, Dallas County, Iowa. Specimen 44106. Five times natural size.

PLATE II. LEPIDOCARPON GLABRUM *Darrah sp. nov.* Figure at top. A lateral section through a seed showing the sporangial wall, the dense "nutritive" tissue, the seed megaspore, and the central cavity. Shuler Mine, Waukee, Dallas County, Iowa. Specimen 44103.

Figure at bottom. A sagittal longitudinal section through an immature seed showing the hard sporangial wall and the gametophyte. The tissues surrounding the central cavity not fully differentiated, although the nature of the "nutritive" layer is suggested. Shuler Mine, Waukee, Dallas County, Iowa. Specimen 44107. Both photographed from cellulose nitrate peels, magnified five times natural size.

Plate I

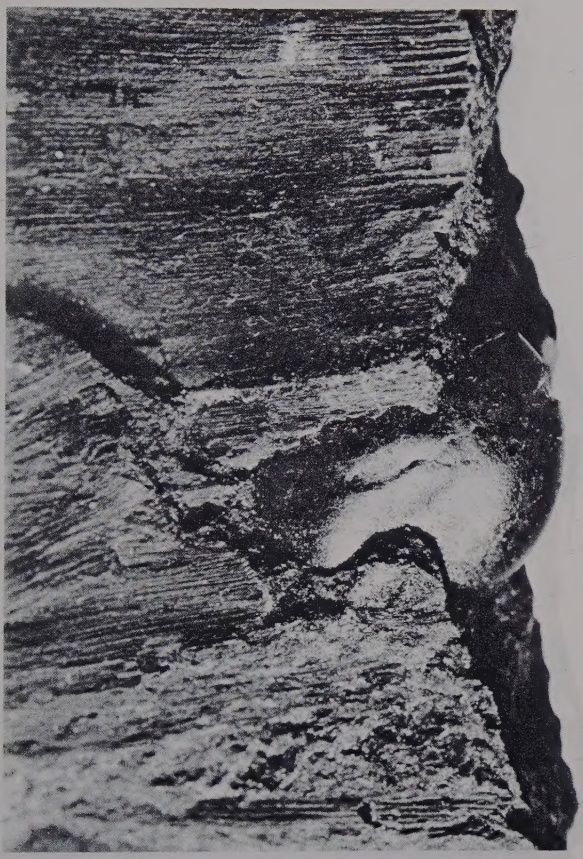
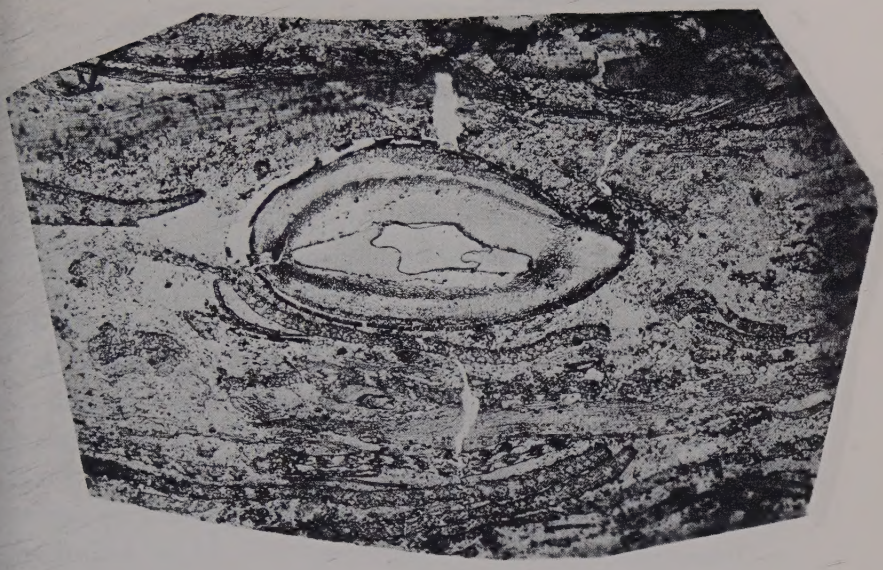
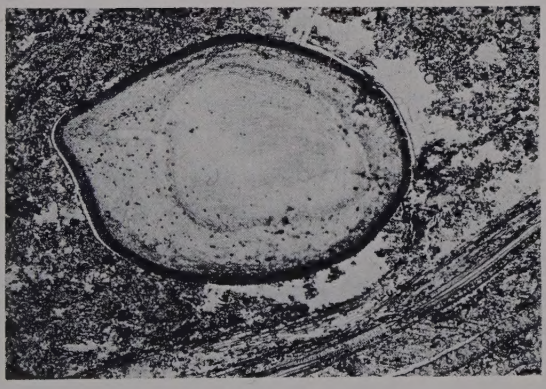


PLATE II





the degree of variation in each form is unknown, and it is convenient to have a purely artificial method of classification. In this manner one may identify with reasonable accuracy a great number of objects without entering into the difficult morphological problem of determining botanical relationships. No attempt is made here to reduce the name *Cystosporites* to a synonymous position.

In 1879, Lesquereux (8) described, under the name of *Lepidocystis*, sporangia which were either isolated or attached to axes of unknown character. He himself said, "The limitations of this genus are vague and uncertain." However, he astutely referred the majority of these peculiar fructifications to the lycopods. The capsules are cylindrical or ellipsoidal and are smooth or angular. I have studied the type series of Lesquereux's species and have recognized two major groups. Sometimes, as in *Lepidocystis fraxiniformis* Lesquereux, many spores are to be found within the sporangium. In other cases, with a single spore, the bladder-like sporangia, which were originally inflated, have been flattened during preservation. In *Lepidocystis vesicularis* Lesquereux, an example of the latter group, the large sporangia are oval or nearly square in outline. The average diameter of this type is 1 cm. The occurrence of impressions of such large sporangial organs in rocks of Upper Carboniferous age, and of a few forms probably related to them in rocks of the Lower Carboniferous age, suggests that some characteristic feature, probably the presence of protective tissues in the sporangial wall, made preservation possible. It should be observed that the sporangial wall of *Lepidocarpon* has such construction.

The recent discovery of a new *Lepidocarpon* has shown an unexpected relationship between *Lepidocystis* and *Lepidocarpon*. Moreover, it is the first case of a *Lepidocarpon* in which the sporangium is shed free from the

sporophyll. The seeds obtained from the Iowa and Kansas coal balls are smooth and lustrous and are protected merely by the thickened cells of the sporangial wall. In other words the isolated "seed" is a sporangium and its contents. There is no suture nor other mechanism for dehiscence. Many thin sections have revealed the presence of a gametophytic body, in which no archegonia have been preserved. The different tissues produced within the sporangium will be discussed in the description of the species given later.

A number of seeds were macerated with dilute hydrochloric acid and the large seed megaspores were recovered. These are ovoid or ellipsoid bodies nearly as large as the sporangium with the megaspore wall thicker at its distal end. They are undoubtedly the same type of spore as that termed *Cystosporites* by Schopf. However, the differences in size between his species (*Cystosporites breretonsis* Schopf) and the isolated spores in coal make it impossible to attribute both forms to a single species. The recognition of the megaspore of our seeds confirms their reference to *Lepidocarpon*.

However, the external form and gross anatomy of these seeds apparently conform in all particulars to the isolated seed-like or sporangium-like bodies described by Lesquereux under the name *Lepidocystis*. A number of the species of *Lepidocystis* are nothing more than the sporangia of *Lepidocarpon* and their contained structures, hitherto only recognized with certainty in examples showing the sporangium associated with its sporophyll. Thus the *Lepidocarpon* ("*Lepidocystis*") from Iowa coal balls illustrates a more mature condition of the seed body than usually observed in the familiar *Lepidocarpon*.

It is therefore consistent with the evidence to refer these fossils to *Lepidocarpon* without amplifying the generic concept. A reference of this form to *Lepidocystis*

would be inappropriate inasmuch as this "genus" includes a variety of unrelated fructifications, some of which are megasporangia filled with large numbers of spores.

The sporangium is similar in its construction to *Lepidocarpon lomaxi* Scott, but the tissues developed within the sporangium show much more detail than in this species. At the proximal end of this seed-like sporangium there is a vascular trace which forks twice, but the four branches quickly exhaust themselves. The bifurcations are at right angles to each other, and by serial sections it has been observed that the two forkings take place one above the other. The individual elements in the vascular trace are spiral tracheids. It is somewhat difficult to identify each of the tissues within this seed. The hard integument is the sporangial wall. It is only one cell in thickness and the palisade-like cells are columnar in longitudinal section with a length two to three times the diameter. In transverse section the cells of the integument are roughly hexagonal, sometimes quadragonal. The cells are usually filled with a dense material, which is sometimes limited to the peripheries of the cell cavities. The functional or "seed" megaspore of typical species of *Lepidocarpon* is frequently accompanied by three abortive spores which are appressed to the triradiate crest of the functional spore. In only a few of our preparations have abortive spores been observed and all of the evidence points to the fact that in life the degeneration of the abortive spores was usually complete. Schopf (11) and Arnold (1) have both observed isolated spores of this type. Schopf correctly identified his spores with *Lepidocarpon* and *Illiniocarpon.* Arnold isolated his specimens from a poorly preserved cone from Mazon Creek, Illinois. In the case of Arnold's specimen (*Lepidostrobus braidwoodensis* Arnold), the spores probably were not those of a *Lepidocarpon.* In the seeds from the Iowa coal balls

only the smaller and more immature forms are recognized as typical *Lepidocarpon*, that is specimens still within an integument. All of the seeds attaining the maximal or near maximal size are found isolated.

LEPIDOCARPON Scott, Phil. Trans. Roy. Soc. Lond. B. vol. 194, 1901.

Lepidocarpon (Lepidocystis) **glabrum** *Darrah sp. nov.*

The seeds are large, 10–16 mm. in length, 8–10 mm. in width and 3.5–4.5 mm. in thickness. The seed body is smooth and lustrous with no ornamentation present. There is a small pit or interruption in the cells of the integument at the base of the seed where the vascular traces have entered. The protective integument is the massive sporangial wall, which is composed of columnar cells, usually filled with a dense substance. Within this integument, towards the center, are four tissues which are conspicuously different from one another. The outer of these is a closely packed tissue composed of rounded, nearly isodiametric cells with rather thick walls, larger in diameter than the columnar cells on the periphery. This tissue is several cells deep. The next tissue is a loose network of rounded parenchymatous cells which are, at maturity, somewhat larger than the preceding. They have thin walls and are frequently irregular in shape. Within this tissue is a closely packed mass of smaller, isodiametric and thin-walled cells, which line the cavity and completely surround the fourth tissue (the gametophyte). The seed megaspore is always present. The megaspore is of the *Cystosporites* type; abortive spores occasionally can be distinguished. In the basal portion of the seed there is a dense pad composed of the second parenchymatous tissue, into which runs a vascular strand that divides twice to form four short strands which soon exhaust them-

selves. This pad of tissue has four club-shaped masses of cells of unknown significance. Presumably from one of these, perhaps from all, megaspores could be developed. I assume that this may be homologous with an archesporial pad. The gametophyte is extensive, nearly filling the whole cavity.

Iowa: Dallas County, Waukee, Shuler Mine. F.O.Thompson Coll.
: Polk County, Walnut Township, Urbandale Mine. F.O. Thompson Coll.
: Lucas County, Williamson Mines 3 and 5. F.O.Thompson Coll.
Kansas: Crawford County, Frontenac. F.O.Thompson and W.C. Darrah Coll.
Carboniferous: Pennsylvanian: Des Moines Series

Summary

The following new observations are believed to offer significant information concerning the Carboniferous lepidodendrids:

1. A portion of the genus *Lepidocystis* Lesquereux comprises isolated seeds of *Lepidocarpon.*

2. The mature *Lepidocarpon* sporangium is shed from the strobilus.

3. In at least one species of *Lepidocarpon* the sporangia are shed free from the sporophyll.

4. *Lepidocarpon glabrum* Darrah is described as a new species, demonstrating these observations.

The knowledge that the lepidodendrids include seed-like forms of remarkable diversity, some of which are shed completely from the parent sporophyll, modifies considerably our concepts relating to those Carboniferous pteridophytic plants which produced the homologues of true seeds. They agree far more closely with the gymnosperm seed, than has been hitherto recognized.

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